

Is phylogenetic and functional trait diversity a driver or a consequence of grassland community assembly?

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Abstract

1. Community assembly changes fundamentally in response to disturbance following habitat destruction due to extreme events and human activities. There are several important aspects of community assembly that can be measured in response to disturbance or during species establishment. Of these measurable outcomes, metrics of taxonomic or species diversity (SD) are perhaps the most common and logistically the easiest to evaluate.
2. It is increasingly evident that measurements of phylogenetic (PD) and functional trait (FD) diversity can provide more information than traditional measures of diversity and desirable and informative metrics to measure restoration outcomes. However, it is unclear whether FD and PD are drivers or a consequence of community assembly.
3. This Special Feature highlights eight field studies and a review that have investigated how PD diversity and functional trait diversity can be used to better understand grassland community assembly following disturbance or during restoration, and how as potential drivers they can be manipulated experimentally or incorporated into evolutionary models. Topics include: colonizing species as a function of FD and PD; dominant species origin impacts on subordinate species FD; impacts of environmental gradients such as seed mix richness, first-year precipitation and restoration age on FD and taxonomic diversity; impacts of drought and resource availability; and a synthesis of studies that measured FD and PD to determine if they provide similar or incongruent inferences for ecological and functional processes.
4. The work in this Special Feature indicates that SD, FD and PD can act as drivers and passengers of community assembly, and often yield different insights. Environmental gradients such as soil nutrients, precipitation and environmental drivers like drought can influence FD and PD of assembling communities in predicted and unexpected ways.
5. *Synthesis.* Results from the studies in this Special Feature highlight the importance of considering a multitude of ecological and evolutionary drivers of community assembly in grassland ecosystems. Studies pushing this field forward will be those that incorporate or study higher trophic levels, realistically incorporate climate change and disentangle the impacts of FD and PD.

KEYWORDS

community assembly, disturbance, functional trait diversity, grassland restoration, phylogenetic diversity, plant community, taxonomic diversity

1 | INTRODUCTION

Community ecologists have long strived to understand what drives community assembly. Theoretical exploits have delved into the roles of competitive exclusion (Gause, 1934; Grinnell, 1904; Tilman, 1990), niche partitioning (Hutchinson, 1959), species filtering (Webb, 2000; Weiher, Clarke, & Keddy, 1998) and neutral assembly (Bell, 2001; Tilman, 2004). Contemporarily, such work is important in the context of ecological restoration and ecosystem recovery after disturbances. Indeed, the United Nations recently declared the next decade “The Decade on Ecosystem Restoration” (United Nations Environment Programme, 2019), highlighting the need to understand the drivers of community assembly, as society strives to build new and repair damaged ecosystems.

To tackle this topic, community ecologists need suitable metrics to understand the processes of community assembly. There are several possible desirable outcomes of community assembly related to ecosystem services, of which metrics of taxonomic or species diversity (SD) are some of the most frequently evaluated measurements of biodiversity. SD is determined by species counts, often weighted by species abundance. However, it is increasingly evident that measurements of phylogenetic (PD) and functional trait (FD) diversity can also reveal important aspects of community assembly beyond inferences that can be drawn from more traditional metrics (Barber et al., 2017; Cadotte, Carscadden, & Mirotnick, 2011; Chao, Chiu, & Jost, 2014; Hipp et al., 2015; Khalil, Gibson, & Baer, 2017; Mokany, Ash, & Roxburgh, 2008). PD is a measure that incorporates the evolutionary relatedness of species in a community, while FD is a measure of the variability in an ecosystem of specific measured traits among species in a community. PD requires knowledge of the gene-molecular structure of co-occurring species in a community. FD requires knowledge of species performance in terms of various characteristics of co-occurring species such as leaf or root construction costs (Laureto, Cianciaruso, & Samia, 2015). Both FD and PD can provide inferences on species niche relationships within a community (Gerhold, Cahill, Winter, Bartish, & Prinzing, 2015; Mouchet, Villéger, Mason, & Moullot, 2010) (Gerhold et al., 2015; Mouchet et al., 2010) and may also provide land managers desirable and informative metrics to measure restoration outcomes (Hipp et al., 2015). However, it is unclear whether FD and PD are drivers (i.e., causal agents) or passengers (i.e., a consequence *sensu* MacDougall & Turkington, 2005) of community assembly. In this Special Feature, ecologists seeking to understand community assembly in grasslands present studies where PD and FD is manipulated or observed and discuss how this knowledge can inform ecological theory, conservation and ecosystem restoration.

Born out of an Ecological Society of America Ignite session in August 2018 in New Orleans, LA, this Special Feature offers insights from new studies that have investigated whether PD and FD can be useful metrics for assessing community assembly, and how they can be manipulated experimentally. Our goal in collating this work

is to provide a link between empirical studies testing plant eco-evolutionary concepts and practical application. Papers in this Special Feature cover experiments where SD, PD or FD have been observed or manipulated allowing for theoretical explorations of the utility of FD and PD for community ecology, with implications for using PD and FD in ecological modelling frameworks. While primarily focusing on grassland plant communities, topics such as the effects of disturbances across continents have implications in other biomes as well. Such broad perspectives on the potential utility of PD and FD as measures of community assembly, of manipulating PD and FD to achieve stated management goals and of theoretical considerations for applying PD and FD in ecological models, have broad implications across ecology. The work collated here is timely as restoration practitioners begin to move beyond traditional SD and look for new tools that are better descriptors of structure and functional potential of restored communities.

2 | HIGHLIGHTS

The nine studies included here span the globe and incorporate a variety of scales from carefully controlled mesocosms to large-scale observational studies of grasslands. The research shows how PD and FD can be experimentally manipulated individually or in tandem, and how they can be measured as responses to changes in environmental context. Some studies looked at different diversity measures as drivers of grassland assembly—they manipulated SD, PD and/or FD. Others viewed diversity as a potential passenger of community assembly and measured diversity consequences of disturbance, edaphic gradients and other environmental drivers. Primary studies represent a range of geographies and ecosystems including California grasslands; North American desert, short, mixed and tallgrass prairies; Mediterranean grasslands; mesic European grasslands; and Mongolian grasslands. The majority of research in this issue is from primary studies with the exception of Cadotte, Carboni, and Tatsumi (2019), who provide a systematic review of studies that measured both FD and PD, and draw conclusions about when they provide congruent or dissimilar insights. In sum, this issue demonstrates various and novel ways to manipulate, measure and disentangle the effects of different diversity metrics and approach diversity consequences and drivers from unique angles.

3 | MEASURES, MANIPULATIONS OF DIVERSITY

Studies included in this issue often used standard measures of species diversity, functional diversity and phylogenetic diversity. Species richness (Barber et al., 2019; Miller, Li, LaForgia, & Harrison, 2019), diversity indices (Barber et al., 2019; Brandt, Seabloom, & Cadotte, 2019) and dissimilarity indices (Barber et al., 2019; Yang et al., 2019) were used to describe SD. Standard functional richness,

evenness, dissimilarity indices and community weighted means were used to describe functional trait composition (Galland et al., 2019; Griffin-Nolan et al., 2019), and intraspecific trait variation was measured to capture impacts of competition (Galland et al., 2019; Khalil, Gibson, & Baer, 2019). PD measures included distance-based pairwise measurements (e.g., mean pairwise distance, mean nearest taxon distance; Barber et al., 2019; Brandt et al., 2019; Yang et al., 2019) and richness-based metrics (e.g., Faith's phylogenetic diversity; Griffin-Nolan et al., 2019). Most studies that measured FD or PD reported standardized effect sizes based on randomization tests to control for species richness.

Though standard indices were often used, researchers often analysed them in unique ways to produce new insights. For example, Perez Carmona, Bello, Azcarate, Mason, and Peco (2019) used the relative interaction index, a standard measure to distinguish between competitive or facilitative interactions through biomass measurements, to ask whether trait effects on competition are due to simple trait dissimilarity or to a trait-based hierarchy of species relative to a competitively dominant phenotype. Importantly, they also show that incorporating intraspecific trait variation improves predictions of competitive outcomes because phenotypic plasticity can reduce the intensity of competition and promote coexistence. Khalil et al. (2019) took traditional intraspecific trait variation measures but compared them across spatial scales (e.g., population vs. community intraspecific trait variation) to measure the extent and strength of external and internal filtering for driving competitive interactions. Galland et al. (2019) measured FD and PD using Rao's index, but used it to understand how trait/evolutionary uniqueness or redundancy impacted colonization. Miller et al. (2019) used unique statistical approaches in their 19-year dataset to address whether FD is a passenger or driver of community assembly following drought.

Many researchers took unique approaches to manipulating diversity or to investigating what impacts it. Galland et al. (2019) manipulated both FD and PD in a fully factorial experiment that sought to look at the impacts of both on colonization. They included an N-addition treatment to explore the impacts of resource availability. The advantage of this novel approach is being able to disentangle FD impacts from PD and vice versa. Results from experimental studies such as this are critical to informing community assembly theory on the interplay between FD and PD. Brandt et al. (2019) used a unique experimental approach—removal of above-ground biomass and N-additions to investigate the dual impacts of disturbance and resource availability. Barber et al. (2019) used 120 tallgrass prairie restorations to explore the PD and SD consequences of a variety of management and climatic variables in an uncontrolled field setting. Griffin-Nolan et al. (2019) manipulated water availability to look at drought over 4 years while Miller et al. (2019) used a 19-year time series to investigate the impacts of real droughts. Lastly, Cadotte et al. (2019) amassed results from 79 studies and 188 comparisons between FD and PD in a review that sought to glean generalities and insights into the relationship between FD and PD in studies across the globe.

4 | DIVERSITY CAN BE BOTH A PASSENGER AND A DRIVER OF COMMUNITY ASSEMBLY

The studies in this Special Feature found a variety of answers to the question on whether PD and FD are passengers or drivers of community assembly. Environmental context seems to play a strong role in the answer to this question, and often results in FD or PD being passengers of assembly. For example, Miller et al. (2019) and Griffin-Nolan et al. (2019) used natural variation in precipitation and experimental drought, respectively, to investigate drought impacts on FD. Both found FD to be a passenger of community assembly changes driven by drought, though Griffin-Nolan et al. (2019) found an increase in functional dispersion and Miller et al. (2019) found a decrease in FD mirrored a loss of species richness driven by drought. Similarly, Brandt et al. (2019) found that SD and PD both changed in response to disturbance and changes in nutrient availability in a field setting, suggesting PD is a passenger to environmentally driven changes in SD. Yang et al. (2019) found that SD was impacted by both water and nutrient additions, but PD was only impacted by nutrient availability. In a greenhouse experiment, Perez Carmona et al. (2019) showed that trait differences determine competition between plants, and these trait effects change under different resource levels, which opens the possibility that it could act as a driver of community assembly that depends in part on environmental context. Khalil et al. (2019) was the only other study here suggesting that FD expressed through intraspecific trait variation can be a driver of community assembly, especially if dominant species impact FD of subordinate species. In contrast, Barber et al. (2019) found no impact of environmental gradients such as restoration age, time since fire, seed mix richness and precipitation in first year of planting on PD, suggesting PD is not a driver or passenger of community assembly.

5 | DIVERSITY MEASURES GIVE DIFFERENT, COMPLEMENTARY INFORMATION

Studies that measured both FD and PD together suggest that these two measures give differing, but complementary information. Galland et al. (2019) found that high levels of FD decreased community resistance to natural colonization—making it a driver of community assembly. However, PD tempered the effect—with high PD, FD did not decrease resistance, suggesting an interplay between them such that both drive community assembly but with their impacts differing depending on each other. Griffin-Nolan et al. (2019) showed a similar pattern, where changes in FD and PD did not consistently match; as functional traits changed from drought-tolerance to drought-avoidance, PD did not differ accordingly. Barber et al. (2019) showed that while PD did not change with environmental context, SD did respond to all the environmental gradients they analysed. Lastly, in their systematic review, Cadotte et al. (2019) found that while FD

and PD are often positively correlated, functional and phylogenetic dispersion sometimes show opposite patterns. Importantly, FD and PD infrequently respond similarly to environmental drivers, supporting many of the findings of studies in this Special Feature.

6 | RESTORATION IMPLICATIONS

It is critical to understand what drives grassland community assembly in order to restore damaged grasslands and create new ones. This information is especially important in the context of ambitious international goals such as the Convention on Biodiversity's Aichi target of restoring at least 15% of damaged ecosystems by 2020 and the United Nations Decade on Ecosystem Restoration. The implications of the studies in this issue for grassland restoration are that competition, seed source and environmental context can all influence taxonomic, phylogenetic and functional diversity in unique ways, emphasizing the importance of accounting for each in seed mix and management decisions (e.g., 2019). Restoration practitioners are largely concerned with taxonomic community composition and assembly. However, studies like those in this issue can help managers predict the impacts of management decisions, invasive species impacts or environmental context on restorations, and attempt to counteract potentially negative impacts. For example, Brandt et al.'s (2019) experimental manipulations are potential restoration strategies that can affect SD and PD outcomes in the resulting communities. As climate change alters precipitation and resource availability, studies of PD and FD here and elsewhere can inform managers which species, evolutionary histories and/or functional traits might be lost, gained or be able to withstand the effects of climate change (Baer, Gibson, & Johnson, 2019).

7 | FUTURE CHALLENGES AND OPPORTUNITIES

While the papers in this Special Feature focus only on plant communities, higher trophic levels are important avenues of study for community assembly, PD and FD research as well. Top-down control of ecosystems has been widely documented (Paine, 1969; Ripple et al., 2014; Schmitz, 2005), so is an important aspect of community assembly that is sometimes overlooked. Direct and indirect interactions from predators and herbivores may be able to explain why field experiments often give different results than carefully controlled mesocosm or greenhouse studies. Incorporating trophic interactions into plant community research and looking at PD and FD of higher trophic levels are both exciting but underexplored areas for future research (Thompson, Davies, & Gonzalez, 2015). Such information could eventually help ecologists build whole-ecosystem models that predict the strongest influencers of FD and PD in any given grassland (Fry et al., 2019; Pappas, Fatichi, & Burlando, 2016).

One especially important trophic interaction in grasslands is that of grazers on plant communities. There has been extensive work done on the different impacts cattle versus bison have on North American grasslands (Knapp et al., 1999; Steuter & Hiding, 1999), and on grazing impacts in African savannas (Eby et al., 2014; Young et al., 2013). Relatively fewer studies have looked into the PD and FD consequences of grazing (e.g., Salgado-Luarte et al., 2019), making it a promising avenue for future research. Such inquiries into both working landscapes like ranches and conservation-oriented projects such as bison reintroductions, will help push science in this field forward.

Climate change is already impacting the world's grasslands and will continue to for the foreseeable future (Gibson & Newman, 2019). This Special Feature has multiple studies on the impacts of drought or altered precipitation on FD and PD, and many more studies that altered resource availability. Climate change impacts are difficult, but not impossible, to comprehensively include in experiments, because they simultaneously impact precipitation, temperature, trophic interactions and phenology. A significant challenge moving forward will be to design and carry out studies that realistically mimic a future world that is currently uncertain.

Moving forward, there are exciting opportunities for growth in this field. Given that FD and PD are often correlated (Cadotte et al., 2019), researchers may be tempted to measure only one of them. However, experimental, real-world and systematic reviews in this issue suggest a more nuanced approach that is necessary. Both FD and PD give us unique, complementary information; Cadotte et al. (2019) suggest that PD may be a good measure for studies interested in highlighting multivariate conserved ecologically similar traits while FD or single traits may be best for highlighting more recent changes or impacts. The experimental manipulation of both PD and FD done by Galland et al. (2019) and others (e.g. Hipp et al., 2018) supports the idea that FD and PD give different information. Such results help push the theory forward and give experimentalists new avenues of exploration as well.

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